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THE NATURE OF GALLERIES FORMED BY INCIPIENT STAGE LARVAE OF *MELANOPHILA CALIFORNICA* VAN DYKE IN PONDEROSA PINE

by
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The Nature of Galleries Formed by Incipient Stage Larvae of *Melanophila californica* Van Dyke in Ponderosa Pine.

INTRODUCTION[1]

The understanding of the nature of incipient flathead galleries is a necessary adjunct to the development of the position of flathead beetles in relation to the insect losses in California eastside forests. Use has been made of the term "incipient" to apply to a type of development apart from that which has been recognized as a flathead infestation in the past. Flathead infestations have been defined primarily on the basis of the rapidly growing larval stages in the phloem and bark, which larvae are associated with the death of the host. It is now recognized that there is a precursory type of infestation, that which has been designated as "incipient". The latter is an infestation found in trees which are still green and show a greater or lesser degree of resistance to the attack. It consists of small larvae which mine in the cambium region, with this activity resulting in scars where the galleries heal over. Mortality of the larvae is very high. Hence in resistant trees there may be a succession of "incipient" infestations, the larvae of which never reach the stage of rapid development which is associated with the death of the tree. On the other hand in susceptible trees, and this susceptibility may be partially the result of continued "incipient" attacks, the "incipient" infestation is succeeded by the type of development generally recognized as a flathead infestation. These two types of infestations are illustrated in Figure 1, a "flathead infestation", and Figure 2, an "incipient infestation". Liberal use of the term "incipient" has been made in referring to "incipient larvae", the larvae involved in these precursory infestations, and to "incipient galleries", the mines resulting from the feeding of such larvae.

Healed incipient galleries represent the result of development of young larval stages in the host tree. In resistant trees this is the only concrete demonstratable effect as compared with susceptible trees where the attack may result in the death of the trees. In connection with the flathead problem as an entity, which has been considered by Salman and Bongberg (1937) and by the writer (1937), this study is concerned with analyzing a condition (the occurrence of incipient galleries) so that its possible effects may be considered. Such effects are considered primarily from a physiological standpoint. This position is taken on the basis of field observations which have tended to show that trees supporting heavy incipient infestations apparently show some signs of weakening. These indications are such factors as color of foliage, needle complement, and general vigor appearance. Consideration is also given to the mechanical effects, since any defects in the wood will have a direct economic bearing. The object of this present study has been to demonstrate the microscopic nature of these incipient flathead galleries, to show what tissue proliferation takes place in response to the feeding of the larvae, and to consider the physiological responses of the

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[1] Acknowledgement is made to the Department of Forestry, University of California, for loan of a sliding microtome, to the Department of Entomology, University of California for use of microphotographic equipment, and to J. E. Patterson of the Berkeley Laboratory, Bureau of Entomology and Plant Quarantine for assistance in making the microphotographs.

host. The importance of such an investigation is predicated on the finding of abundant incipient galleries in the trees of the eastside forests. If such galleries do not affect the host in any manner, their present distribution warrants a determination of such effects. In the study reported herein the investigation has been limited to the nature of incipient galleries in the wood. Each gallery has, however, a counterpart in the phloem, the nature and effect of which should also be considered.

Background of Incipient Flathead Gallery Studies

Beginning with the observations of A. D. Hopkins, the insect problem in the west has largely been considered a barkbeetle (*Dendroctonus* and *Ips*) problem. However, Hopkins (1899) noted the presence of flatheads in the insect composition and recognized their possible importance. In the case of *Abies nobilis*, Hopkins examined insect-killed trees which had been dead for some time. He concluded "from the character of their work on the outer sapwood that it must be a Buprestid (which had caused the death of the trees), possibly belonging to the genus *Melanophila*. Many (galleries?) had healed over before the trees died, thus producing conclusive evidence that they were attacked while living and probably while in healthy condition." Healed incipient flathead galleries are the only evidences of a flathead attack that would remain on the outer sapwood. Hopkins believed that the nature of flathead attacks warranted a special investigation, and that the subject was one which would demand considerable attention in the future.

The observations of Burke can also be tied in with the study of incipient flathead galleries. In connection with some biological notes on flathead species which attack and kill some of our most important coniferous trees, Burke (1919) writes as follows:

"A curious injury to sugar pine and yellow pine timber in northern California consists of a brown, pitchy, irregular scar several inches in diameter from which radiates small, winding, pitchy lines. The forest pathologists consider the central scare to be caused by a light or diffused stroke of lightning which slightly separates the bark and wood. The radiating lines are the mines of *Melanophila* larvae whose mothers were attracted to the scars to lay their eggs. When the attack failed the larvae died and the new growth covered the wound, forming the curious defect".

The winding lines described by Burke are clearly what are termed incipient galleries at the present time. The interpretation of field observations of the 1936 season and the results of the present study have resulted in an explanation reverse to that made by Burke. It has been found that the incipient galleries run *into* the pitch scars and are their cause rather than the result of their existance.

Up to the 1935 field season incipient flathead galleries had been practically disregarded although they were frequently recognized in connection with pitch scars. Accumulation of notes and stem analysis records of the past few years has led to the recognition of flatheads as an integral part of the forest insect problem (Salman and Bongberg, 1937). On this

basis a study of flatheads was initiated during 1936. Early during the field season, in looking for flathead infestations, J. M. Miller and K. A. Salman of the Berkeley Laboratory were impressed by the abundance of healed, warty galleries at the end of which young flathead larvae were feeding. The term "incipients" was coined for these galleries, and, as a result of these observations, the investigation of such scars was made an important part of the field program. The studies made under this program have been reported on by the writer (1937).

Literature

The literature dealing with such a problem is conspicuous by its scarcity. A few papers dealing with abnormal wood and wound tissues have given some indication as to the nature of hypertrophied development.

According to Somerville (1916) anything which upsets the normal physiological functions of the cambium may apparently result in the formation of abnormal wood. Somerville's studies dealt with the formation of abnormal wood due to heat and excessive drought. In the case of Japanese larch (<u>Larix leptolepis</u>) he found the following characteristics of abnormal wood:

a. Irregular course of medullary rays composed of swollen and greatly elongated cells, frequently discontinuous with rays of previous ring;

b. Abnormal zone largely composed of parenchymatous tissue, which cells appear to produce large quantities of resin;

c. Rays become filled with resin;

may
d. Parenchyma cells/become elongated vertically but are more commonly distorted laterally;

e. Lumina not completely surrounded by cell wall in many cases;

f. Rays tend to split and appear bifurcate in tangential section;

g. Zones of abnormal wood constitute lines of weakness and lumber will exhibit "ring shake".

The production of resin is apparently intimately associated with any abnormality in coniferous species. Conifers attacked by the shoe string fungus rot (<u>Armillaria mellea</u>) produce a greater number of resin ducts than is normally found. <u>Cedrus deodara</u> produces resin ducts which are normally entirely absent. The same is also true for <u>Abies amabilis</u> infected by the witches broom fungus. Somerville refers to Hartig (1892) who found abnormal wood resulting from nun-moth defoliation of spruce. A considerable number of cells in the year following attack were intermediate between normal tracheids and wood parenchyma.

Kuster (1903) gives an extended discussion of the nature of wound wood in his "Pathological Plant Anatomy" (translated ed.). Wound wood deviated from normal wood according to whether its formation is brought about by cross cuts into the cambium or by longitudinal wounds. In longitudinal wounds the cells are wide and the ducts are more numerous than in normal wood. In wound tissue the cambial cells divide perpendicular to the longitudinal axis resulting in short-membered cells. The number of cross walls increases with nearness to the point of injury. Daugher cells of the cambium short-celled zone produce tissue composed of polyhedric parenchyma. The separate cells of such tissues resemble cells of the medullary rays. A few of these cells may become parenchymatic tracheids through thickening of the cell walls. Kuster classifies the above as primary wound wood, which is followed by a zone of secondary wound wood. In the latter the newly produced cells gradually assume a normal form. In wound tissue parenchymatic elements become more prominent the greater the wound stimulus that acts on the cambium. Parenchymatic elements are full of sap and this wood is less resistant to injuries of various kinds (frost, parasites, etc.) than is normal wood. Kuster also refers to the abundant production of resin ducts in wound wood.

Materials and Technique

All specimens used for microscopic study were selected and fixed at the Hackamore Field Laboratory during the summer of 1936. Selected pieces were cut and immediately placed in an alcohol-formalin-acetic acid mixture. The samples were stored in this preservative until the end of the field season. At that time the samples were transferred through an alcohol series to 100 percent alcohol and placed in an aspirator to remove all air from the interior of the wood blocks. The material was transferred to ether-alcohol and then through a series of increasing percent celloidin solutions. The embedding matrix was approximately 12 percent celloidin. Embedded blocks were stored in glycerin-alcohol until sectioning was done. The sliding microtome which was used for sectioning was furnished through the courtesy of the Department of Forestry, University of California. All sections were cut at a thickness of 40 μ. Cut sections were stained with Haedenhain's Haematoxylin and counterstained with Safranine Y. Canada Balsam was used as a mounting medium. The microphotographs presented in conjunction with the following discussion were taken by J. E. Patterson and the writer. Equipment for microphotography was made available through the courtesy of the Department of Entomology, University of California.

Macroscopic Aspects of Incipient Flathead Galleries

The course of the incipient gallery actually begins in the bark where the egg has been deposited. Apparently the newly hatched larva mines directly to the cambial region. The first part of the gallery in this region is very tiny, line like, and almost invisible, gradually increasing to a more easily discernible size. The feeding of the larva runs in a general horizontal direction. In response to the scoring of the wood and phloem by the larvae the host tissues proliferate

and heal over the wounded area. From this activity arises the characteristic winding ridge scars which remain as evidence of the incipient infestation. An illustration of these scars has been given in Figure 2. Living larvae represent potentially successful infestations, with subsequent development giving rise to the flathead infestation illustrated in Figure 1. High mortality, however, results in a great number of unsuccessful incipients, a term applied to the numerous galleries at the end of which no living larva is found. At the point where death of the larva occurred one of two conditions is found: either a small, bird's eye pitch nodule, as shown in Figure 2, or a definite pitch "blister". The latter is apparently associated with the death of the larva at that point where, if it had been successful, its development would have carried it out of the incipient stage. This condition is shown in Figure 3, an example of current mortality which would result in a pitch "blister" and Figure 4, an example of a pitch "blister" formed as the result of the death of a larva in the past. Such resined areas which subsequently are overgrown by the wood, may be up to several inches in length.

Discussion of Microscopic Observations

Normal Wood Structure:

It is desirable to point out several characteristics of normal wood structure in ponderosa pine, since it is these characteristics which are affected by flathead galleries. The line of demarcation of yearly growth is clear-cut. There is a clear distinction of spring and summer wood although the respective amounts of each varies greatly from year to year. Resin ducts are scattered and of moderate abundance. Medullary rays are continuous through the wood growth of several to many years. These features are illustrated in Figure 5a; a higher magnification of a portion of the same section is shown in Figure 5b.

Area of Current Feeding of Incipient Larva:

At the point where feeding is taking place, before any proliferation of cells occurs in response to the injury, a degree of resining is found which is probably somewhat dependent upon the extent to which the wood has been mored. Examples of this resining are shown in Figures 5a and 5b.

Spread of Resining Effect Resulting from Feeding:

The flow of resin in response to the injury caused by the larva is not confined to the limits of actual feeding. Resining spreads either side of the gallery by at least as much as the width of the gallery itself. Figures 6a and 6b (a higher magnification) show this spread of resining in radial section.

Healing of Incipient Galleries:

The external appearance of healed galleries has already been demonstrated. Microscopic examination of such healed lesions shows that there is an area of abnormal tissue formation at the point of injury

peripheral to which the wood tissue again become normal. An example of a recent injury (1935) which has healed over is shown in Figure 7. These healed lesions remain a permanent record in the wood and frequently evidence is found of an incipient attack extending back over a considerable period of years. In Figure 8 three galleries which lie deep in the wood are illustrated.

Our interest lies in the features which characterize these healed lesions:

Development of parenchyma tissue and resin infiltration:

The first growth response to the injury is the proliferation of parenchyma cells which, in contrast to normal wood tracheids are thin-walled and irregularly polygonal and become heavily infiltrated with resin. The lumina of such cells are much larger than the lumina of normal wood tracheids. Considerable variation in the amount of parenchyma has been found, probably the amount varying with the degree of injury sustained. Examples of parenchyma development are shown in Figures 7 and 9, in which the resin infiltration should particularly be noted. In many instances the resining completely hides all cellular structure as is shown in Figures 7 and 9. In older lesions in the wood the individual parenchyma cells do not stand out as clearly but the resin infiltration is a permanent characteristic. Figure 10 shows a portion of an old lesion in which resining is the outstanding characteristic.

Effect on medullary rays:

Two effects of the injury on medullary rays were evident. One was the discontinuity of the rays as resulting from the area of parenchymatous tissue and the second, the resin infiltration of the rays. In nearly all of the section examined the lesion constituted an effective block to normal ray passage from one growth layer to the adjacent one. This feature is effectively demonstrated in Figures 7 and 9. Good examples of the resin infiltration into the rays is shown in Figures 11a and 11b. These figures may indicate that the rays tend to vary at the point of injury from their normal uniseriate character, but owing to the density of resining this point could not be accurately determined.

Wood growth peripheral to area of parenchymatous development:

External to the area of parenchymatous tissue production wood tracheids once more appear. The first tracheids laid down may be of abnormal appearance, perhaps due to a transitional nature between parenchyma and wood tracheids. Reference is made to Figures 7, 9, and 11b, for illustration of this point. It is evident that at least the tracheids do not at once assume their normal regular nature. It will be noted in Figure 9 and also Figure 12 that some of these first wood tracheids peripheral to the injury have lumina which are elongated tangentially. When such sections are viewed under sufficiently high magnification the bordered

pits in the aspect usually presented in radial or tangential section. The interpretation of this condition is that the wood tracheids have been displaced horizontally. Although no definite cause can be assigned to this phenomenon it is possible that the disruption of normal pressure relationships by the lesion may have resulted in the displacement.

<u>Rate of growth in relation to lesions:</u>

In examining older lesions it was noted that the growth in the year of injury, at the point of injury, was less than that either side of the gallery, resulting in a concavity in the growth. However, in the year following the growth directly peripheral to the point of injury was greater than that either side so that at the end of this second season the growth was evened off. An example of this condition is given in Figure 13. A similar tendency is shown in Figure 9 where the line demarcing the end of growth of the season in which the injury occurred is fairly even, although the line of development of parenchymatous tissue is most uneven. It is probable that this type of development is more marked where the injury is less severe since a severe injury results in the very warty., protruding type of healing.

<u>Resin duct formation:</u>

A condition referred to in the literature reviewed was found to be prevalent in the material examined, namely, an abundance of resin ducts. The normal distribution of resin ducts has already been mentioned in reference to Figure 5a. In Figures 14, 15, and 16 this abnormal condition is illustrated. In each case there has been a development of numerous resin ducts immediately peripheral to the injured area. Possibly this tendency to form resin ducts in this region is related to the amount of resin present in the area of injury.

<u>Formation of pitch blisters:</u>

The development of a pitch blister was investigated in a series of sections (Figure 17-20 incl.). It was not possible to determine what factor determines whether or not a pitch blister forms at the end of an unsuccessful incipient gallery. The formation of the blister is characterized by an initial parenchyma development such as occurs all along the line of the gallery. The resin flow covers and infiltrates this region, and extends over a varying amount of the surrounding wood tissues. Healing over of this blister begins at the edges and progressively covers the entire resined area, with the tracheids assuming their natural form. In some cases, such as illustrated in the series of Figures 18-21 inclusive, the larval mine has doubled back with feeding occurring in the tissues healing the lesion of the previous season, In such cases the pitch blister covers a considerable horizontal expanse of the gallery. In normal lesion healing the wood tissues central and peripheral of the injured area are unified by the parenchymatous development. However, in the case of formation of pitch blisters there results a separation of wood layers by an accumulation of resin. Such a condition may be expected to make for structural

weakness in the wood involved. The formation of pitch scars in relation to the incipient galleries clearly demonstrates that Burke's interpretation was reverse of the actual conditions.

Comparative anatomy of various portions of an incipient gallery:

The series of Figures 5-7 inclusive, illustrate the condition obtaining in various parts of the same gallery, namely: the current feeding area (Figure 5a and 5b), the partially healed lesion where feeding took place earlier in the same season (Figure 6a and 6b), and the completely healed lesion where feeding took place during the previous season (Figure 7).

Effect of Incipient Galleries on Host

Mechanical:

The presence of any structural abnormality in wood may be expected to have some effect upon the mechanical properties. The presence of incipient galleries in themselves does not necessarily imply any serious mechanical defect in the wood although the possibility exists of "ring shake" due to zones of abnormal wood, as mentioned by Kuster. However, the two types of endings of galleries, bird's eye pitch nodules, and pitch blisters do present a defect which is reflected directly in economic considerations. Lumber which is filled with the bird's eye defects may be degraded accordingly, while lumber in which numerous pitch blisters occur is generally considered to be weakened and hence the economic value is lowered.

Physiological:

Field examinations and microscopic studies have demonstrated the nature of incipient flathead attacks. When a green tree is attacked the mortality of larvae is high, but indications are that the attack is repeated in successive years. The result is a series of healed galleries in the growth rings of the tree. These galleries are frequently accompanied by numerous pitch blisters since pitching out seems to be one of the chief causes of unsuccessful incipient development. The abnormal nature of the tissue which heals over the galleries has been demonstrated. Accordingly, it may be assumed that any such areas interfere to a greater or lesser extent with the normal translocation of food materials. This conduction upward from the roots takes place in the outer growth layers of a tree. Obviously any interference with this conduction column will adversely affect the physiological state of the host. The extent of this effect will depend upon the abundance and distribution of the abnormal non-conducting tissues. It is assumed that resin infiltrated parenchyma cannot carry out the normal physiological functions of wood tracheids. Incipient flathead galleries are disposed in a general horizontal direction. Thus their effect is greater than if they were vertically disposed. Where any considerable abundance of galleries occurs the interference with normal physiological functions could be a factor of importance. It is not contended by any means that this factor is alone in its adverse effect upon

the host. Drought conditions, for example, may be equally, or at times, more important. Rather the contention is that the addition of an adverse biological factor to the environmental complex of the host may create a condition detrimental to the vigor of the tree. Obviously no definite statement can be made as to the specific importance of flathead incipient galleries. As in any other complex of environmental factors any single factor may be the key one at a particular time. As the various factors change so do their interrelations change and the resultant effect upon the tree.

Summary of nature of incipient flathead galleries.

An investigation of the nature of incipient flathead galleries has been made with view to determining their anatomical characteristics as well as their mechanical and physiological effects.

The following salient features characterize incipient flathead galleries:

1. A light flow of resin occurs at the point where the larva is feeding.

2. This resin flow spreads either side of the actual point of injury.

3. The lesioned area heals over in the wake of the larva. There is an area of abnormal tissue peripheral to which the wood structure is again normal. The following points characterize this healing:

   a. The proliferation of parenchymatous tissue is the first growth response to the injury. This tissue becomes infiltrated with resin.
   b. The continuity of the medullary rays is broken by this area of parenchymatous tissue, and the rays themselves may become infiltrated with resin.
   c. Peripheral to the parenchymatous tissue wood tracheids are again laid down. There may be a zone in which the cells are transitional between parenchyma and tracheids, and in some cases the first tracheids are horizontally dislocated.
   d. Growth at the point of injury may be less than normal, and in such cases growth in the following year is greater than normal so that the line of growth is evened up.
   e. An abnormal abundance of resin ducts may develop immediately peripheral to the lesion.
   f. The gallery may end in the formation of a pitch blister.

Conclusions

The interpretation of the nature of incipient flathead galleries is but one more step in an understanding of the entire flathead problem. A condition has been demonstrated whereby the tree may be adversely affected

The question then arises as to whether the tree is weakened by unfavorable environmental factors and then attacked by flatheads which further weaken the tree, or whether the flatheads attack a healthy tree and this attack results in its weakening. However, in light of a summary of published and unpublished notes on *Melanophila* (Salman and Bongberg, 1937), a recent study of the biological and host relationships (West, 1937), and the results of the present investigation, the place of flatheads in the forest insect complex cannot be ignored.

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Figure 1

A typical flathead infestation. Galleries of Melanochila sp. in the bark of Jeffrey pine. Photo by J. E. Patterson.

Figure 2

A typical incipient infestation. A heavily infested specimen of outer wood of ponderosa pine. Ridges indicate course of galleries some of which are completely embedded. Photo by K. A. Salman.

Figure 3

Mortality of an incipient stage larva, with injury to wood which would result in the formation of a pitch blister. Photo by K. A. Salman

Figure 4

itch blister formed at he end of an incipient allery. Photo by K.A. alman.

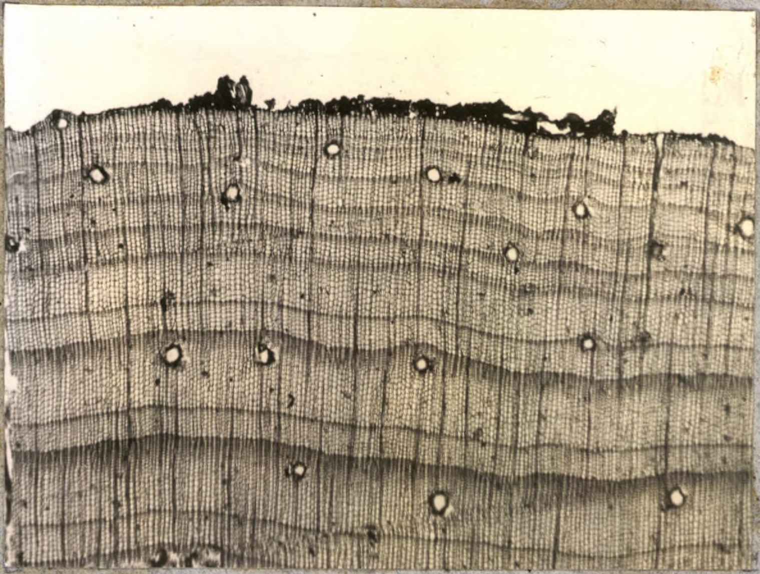

Figure 5a
X-section; x15. Resining at point where larva is feeding on the outer wood. Normal wood structure and distribution of resin ducts is shown.

Figure 5b
X-section; x40. Higher magnification of a portion of the same injury shown in 5a.

Figure 6a
Radial-section; x20. Spread of resining beyond point of actual injury; resin infiltration of parenchyma at point of injury.

Figure 6b
Radial-section; x50. Higher magnification of a portion of the same injury shown in 6a.

Photos by A. S. West and J. E. Patterson

Figure 7

X-section; x16. Proliferation of parenchymatous tissue and resin infiltration of same where feeding occurred; development of normal wood beyond parenchymatous tissue.

Figure 8

X-section; x10. Grouping of three old lesions in the wood as evidence of attack in years past.

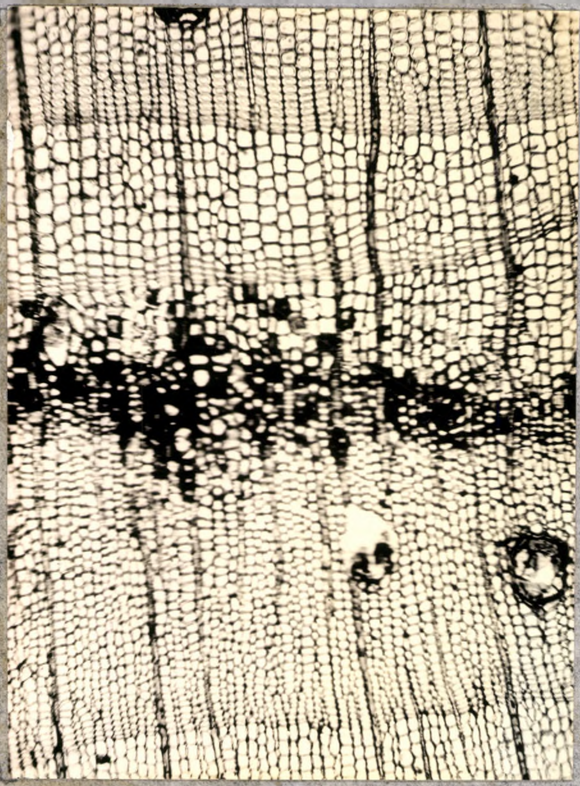

Figure 9

X-section; x40. Parenchymatous tissue at point of injury; horizontally displaced tracheids peripheral to parenchyma; discontinuity of medullary rays.

Figure 10

X-section; x40. Portion of old lesion in wood; resin infiltration of parenchymatous area; discontinuous medullary rays.

Photos by J. [illegible] Patterson and A. [illegible] West

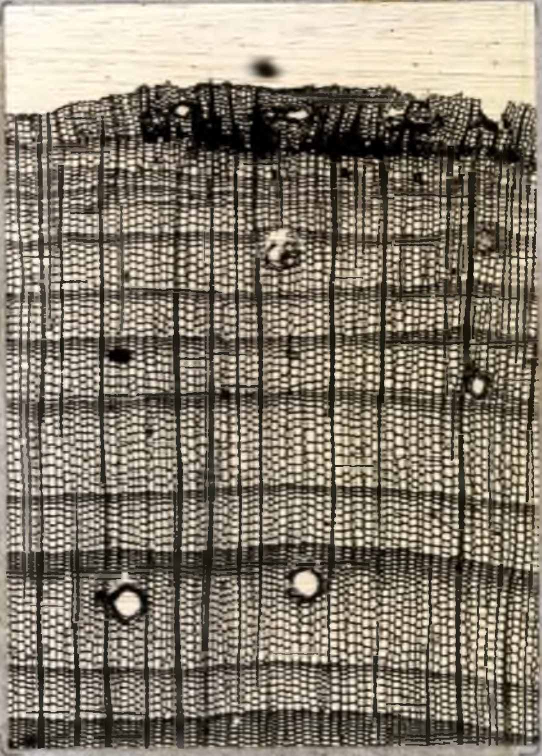

Figure 11a
X-section; x10. Resin infiltration of medullary rays.

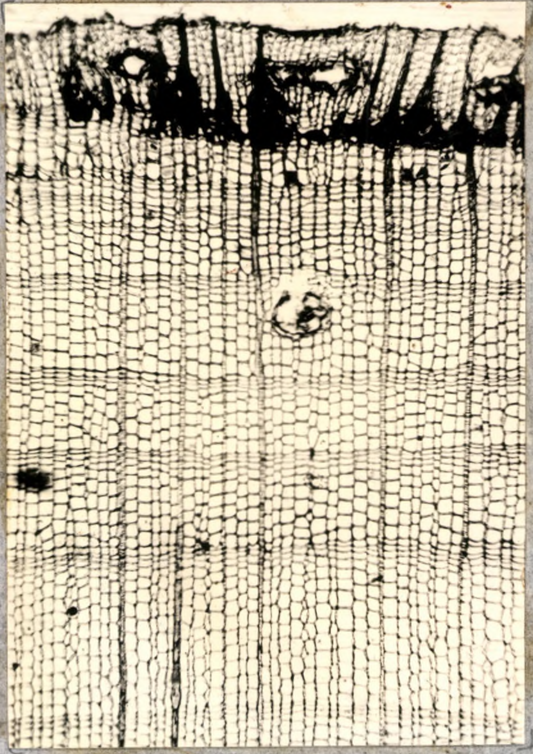

Figure 11b
X-section; x50. Higher magnification of a portion of the same section shown in figure 11a.

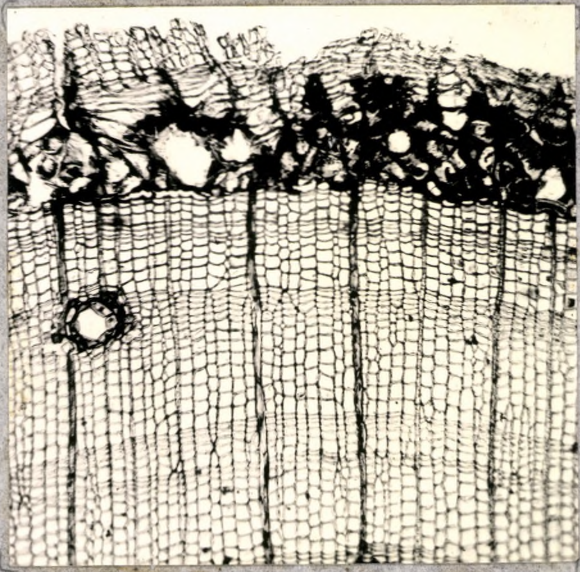

Figure 12
X-section; x40. Resin infiltration of parenchymatous tissue; horizontal displacement of wood tracheids.

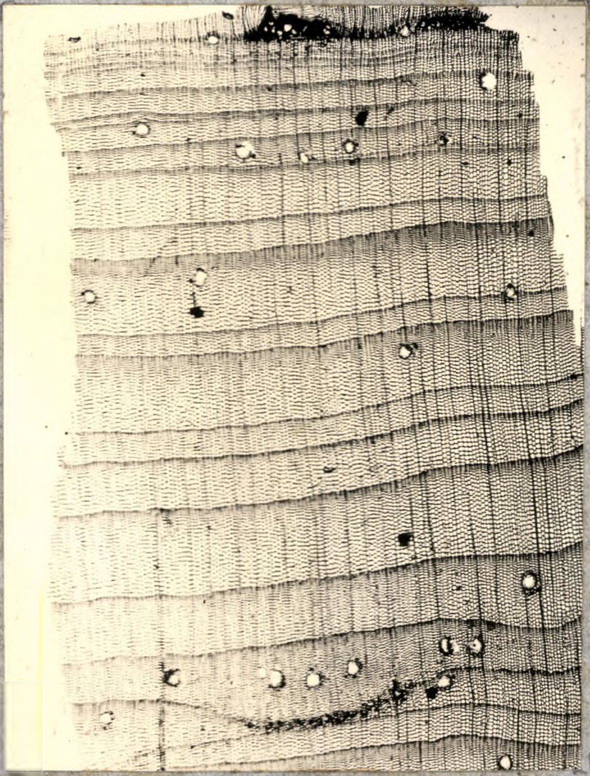

Figure 13
X-section; x14. Old and new lesion in wood; resin ducts abundant peripheral of old injury; evening up of growth line peripheral of old injury.

Photos by A. E. West and J. E. Patterson.

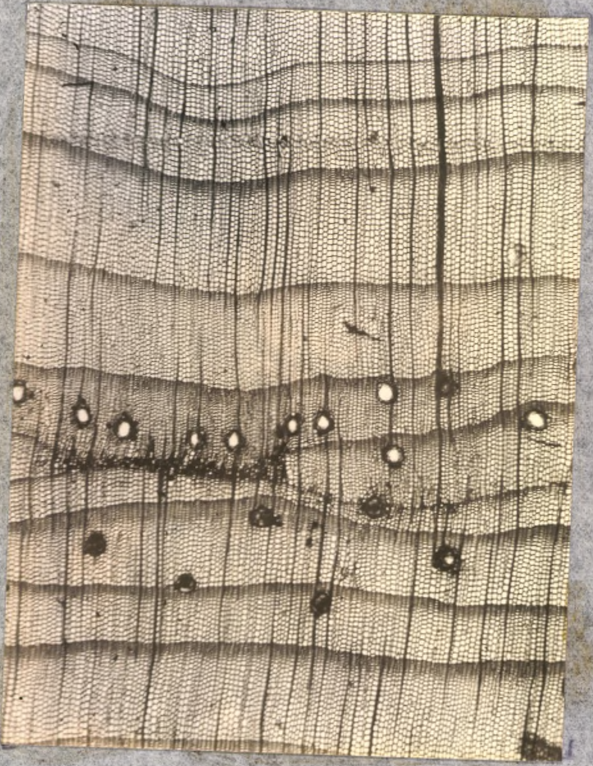

Figure 14
X-section; x25. Abundance of resin ducts peripheral of lesion.

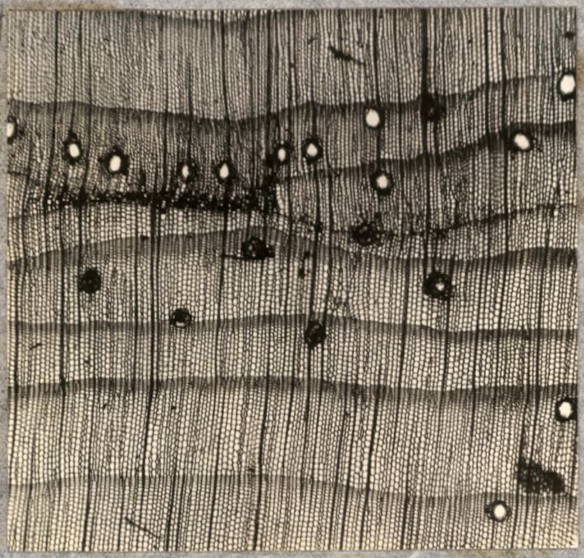

Figure 15
X-section; x25. Abundance of resin ducts peripheral of lesion, and normal resin duct distribution central of lesion

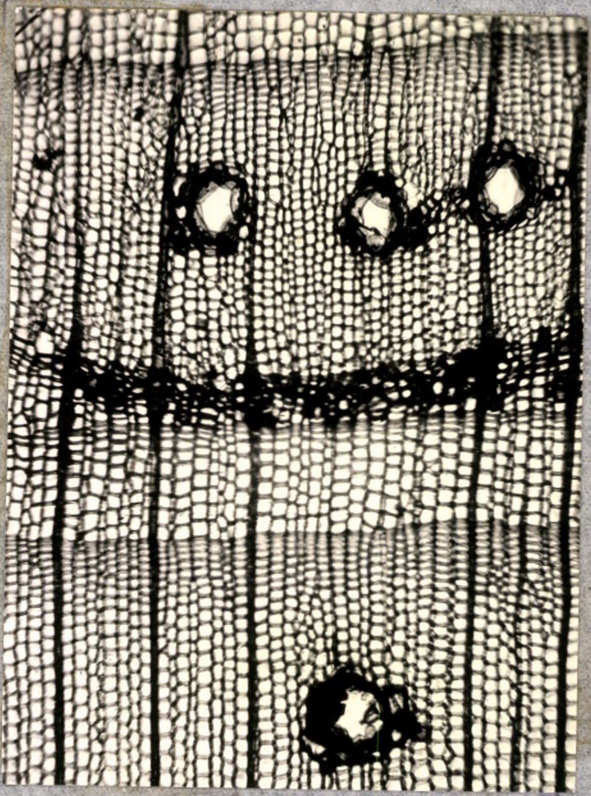

Figure 16
X-section; x60. Resin ducts peripheral of lesion.

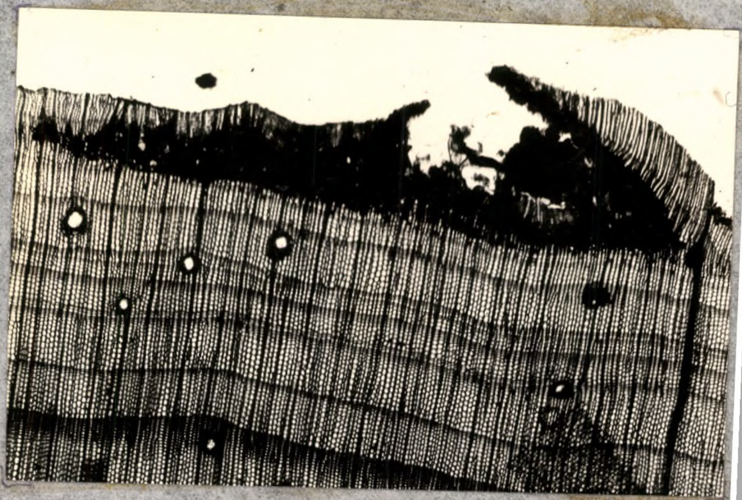

Figure 17
X-section; x20. Formation of pitch blister at upper edge of blister. The original injury was made during the 1935 season and normal healing began. This healing is shown in the second wood layer extending partially over the cavity. In 1936 the larva doubled back and was pitched out by the heavy resining. The outer layer of wood is the growth of the 1936 season beginning to heal over the edge of the pitch blister.

Photos by A.E.West and J. E. Patterson

Figure 18

X-section; x55. Higher magnification of the injury shown in Fig. 17; area of parenchymatous tissue is where the larva fed in 1936; wood tissue healing over the 1935 lesion is shown on the left; outer layer of tissue is 1936 wood extending over edge of blister. Photo by J. E. Patterson and A. S. West

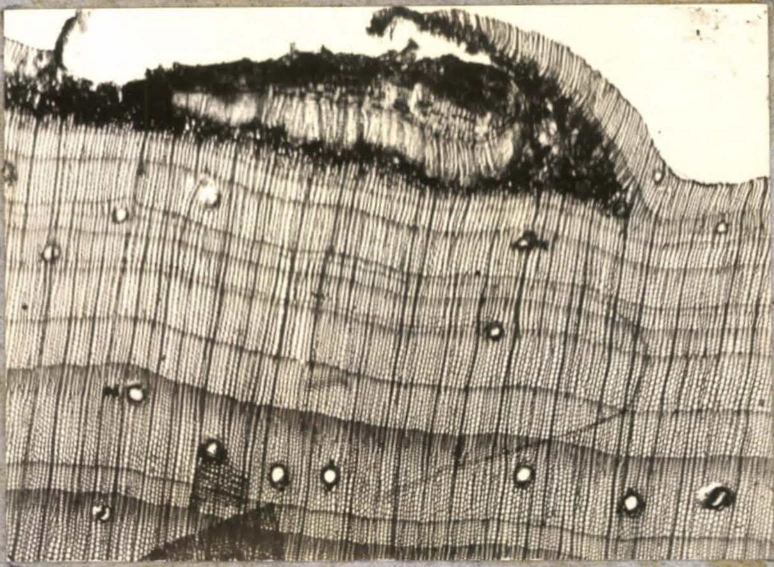

Figure 19

X-section; x15. Section through central portion of pitch blister showing same features as Figures 17 and 18. Photo by J. E. Patterson and A.S. West.

Figure 20

X-section; x55. Higher magnification of a portion of the same area showwn in Figure 19. Photo by J.E. Patterson and A. S.West.